
A Synopsis of the Panamanian Species of *Ilex* (Aquifoliaceae)

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ABSTRACT. The species of *Ilex* (Aquifoliaceae) native to Panama are treated in a synoptic fashion. Three new species are described: *Ilex fortunensis*, *Ilex maxima*, and *Ilex stellata*.

The *Flora of Panama* (Edwin, 1968) listed four species of *Ilex* for the country, based on only 17 specimens. One-half of these specimens were of the widespread *Ilex guianensis* (Aublet) Kuntze collected in the Pearl Islands. An increase in collecting activity over the past 20 years, especially in the moist uplands of Chiriquí, Coclé, and Bocas del Toro, Panama, has produced a current collection base of over 200 specimens representing 10 species of *Ilex*, including three previously undescribed.

Similar changes in estimates of local species diversity for the genus based on new collections occur elsewhere in the Neotropics. For example, extensive collecting in the Guayana Highlands since the 1950s has increased recorded diversity from 6 species of *Ilex* (Wurdack, 1961) to 55 species (Edwin, 1965) to 78 species (Steyermark, 1988). The typological species concepts employed by the latter two authors probably overstate diversity for the Guayana Highlands. The pattern of increase in recorded diversity is indisputable, however, and strongly suggests the need for additional collecting.

In Panama, three main groupings of species can be made based on the nature of the inflorescence-bearing shoots. One group, composed of *Ilex costaricensis* J. D. Smith and *I. pallida* Standley, bears solitary, axillary inflorescences in both flower and fruit. This is equivalent to the solitary flowering unit composed of secondary dichasia sensu Loizeau (1992: figs. 2h, 13). These two species differ from each other in a number of characters and are not closely related.

In the second group the inflorescence-bearing shoots are short while in flower (= brachyblasts), but usually expand and develop normal leaves toward the apex as the fruits mature. In the terminology of Loizeau (1992: figs. 2g, 11, 12), these

are proliferating thyrses. This group consists of four species in Panama: *I. stellata* W. J. Hahn, *I. fortunensis* W. J. Hahn, *Ilex lamprophylla* Standley, and *I. guianensis*, which may be loosely related to each other. The first two taxa are endemic to Panama and are known from only a few collections. *Ilex lamprophylla* is largely restricted to Panama and Costa Rica, with a few isolated populations in Nicaragua. Related species are found in northern South America. *Ilex guianensis* is the most widespread member of a large species group centered in northern South America (Hahn, 1988).

A third group of species includes *I. vulcanicola* Standley, *I. chiriquensis* Standley, *I. yurumanguinis* Cuatrecasas, and *I. maxima* W. J. Hahn. These species are characterized by abaxial leaf punctations and inflorescences borne on brachyblasts in both flower and fruit. The basic inflorescence unit is still a cyme, but the stem that bears the cymes fails to elongate as in the previous group and never bears leaves. The overall appearance of the cluster of cymes is umbellate or paniculate which corresponds to the non-proliferating thyse of Loizeau (1992: fig. 10). The species form part of a natural group probably referable to Loesener's series *Paltoria*. This group of closely related species forms several grades that show broad continua of character states in leaf size and shape, inflorescence size and branching, and fruit size. Several collections show intermediate combinations of character states, making species identification difficult (see notes under *I. chiriquensis* and *I. yurumanguinis*). As most species in this group are South American in distribution, a revision of the group in its main range will be necessary before the identities and relationships of the Panamanian taxa are completely resolved.

Edwin (1968) reported *I. macfaydenii* (Walper) Rehder as possibly occurring in Panama, but this species is restricted to the Greater and Lesser Antilles and possibly Mexico. It is distinguished by thin leaves with long-acuminate apices, distinctly serrate leaf margins, and generally solitary inflorescences.

KEY TO THE SPECIES OF *ILEX* IN PANAMA

- 1a. Leaves epunctate abaxially; individual cymes solitary in the leaf axils when in fruit.
 - 2a. Leaf margin entire or essentially so.

- 3a. Leaves coriaceous, moderately to faintly discoloured, glaucous, glabrous or with a few scattered hairs, the margins revolute, secondary veins obscure to apparent; pistillate cyme branched or unbranched, peduncles 1–2 mm diam.; fruits 3–7 mm long, 2.5–7 mm diam.
- 4a. Leaves elliptic, drying dark brown or black abaxially, the margin revolute, strongly so at the base, venation brochidodromous, secondary veins apparent; cymes solitary in the leaf axils when in flower and in fruit; pistillate flowers 3–7 per dichasium (sometimes solitary at high elevations); fruits 3–7 mm long, 2.5–5.5 mm diam. 1. *Ilex costaricensis* J. D. Smith
- 4b. Leaves usually spatulate or obovate, drying olive green or brown abaxially, the margin revolute but not at the base, venation semicraspedodromous, secondary veins obscure; cymes clustered on brachyblasts when in flower, usually solitary when in fruit; pistillate flowers solitary; fruits 4.5–6 mm long, 4–7 mm diam. 2. *Ilex guianensis* (Aublet) Kuntze
- 3b. Leaves chartaceous to thin coriaceous, strongly discoloured, puberulent, the margin flat, secondary veins distinct; pistillate inflorescence branched, peduncles 2–3 mm diam.; fruits 0.9–1.1 cm long, 0.7–1 cm diam. 3. *Ilex fortunensis* W. J. Hahn
- 2b. Leaf margin toothed or crenulate, sometimes minutely so, the teeth bearing small marginal spines.
- 5a. Leaves planar, elliptic to ovate or obovate, 3–6 cm long, 1.5–3 cm wide, glabrous or pubescent with simple hairs.
- 6a. Leaves drying pale green or olive, margin serrate-dentate, petiole 2–5 mm long; cymes solitary in flower and fruit; fruits 6–10 mm long, 4–8 mm diam. 4. *Ilex pallida* Standley
- 6b. Leaves frequently drying dark brown or black, margin crenulate or serrate to almost entire, petiole 3–45 mm long; cymes clustered or solitary in flower, usually solitary in fruit; fruits 3–6 mm long, 3–4 mm diam.
- 7a. Leaf margin usually distinctly crenulate, flat; petiole 3–8 mm long; cymes clustered on brachyblasts in flower; pistillate flowers solitary; pericarp thin, fruit usually deeply ribbed when dry 5. *Ilex lamprophylla* Standley
- 7b. Leaf margin mostly entire, a few spines occasionally present, never crenulate, revolute, strongly so at the base and abaxially along the petiole; petiole 8–45 mm long; cymes solitary in the leaf axils when in flower; pistillate flowers solitary or more frequently 3–7 per dichasium; pericarp leathery, fruit surface smooth when dry 1. *Ilex costaricensis* J. D. Smith
- 5b. Leaves deeply to shallowly bullate, broad elliptic to rotund, 5–10 cm long, 3–8 cm wide, bearing deciduous stellate hairs 6. *Ilex stellata* W. J. Hahn
- 1b. Leaves with conspicuous glandular punctations abaxially; cymes in flower and fruit borne clustered on brachyblasts.
- 8a. Leaves coriaceous, 1.5–10 cm long, orbicular to elliptic or obovate, secondary venation usually obscure; staminate cymes unbranched.
- 9a. Leaves 1.5–3 cm long; 5–10 cymes per fascicle; fruits 2.5–4 mm long . . . 7. *I. vulcanicola* Standley
- 9b. Leaves 3–10 cm long; 5–20 cymes per fascicle; fruits 4–7 mm long . . . 8. *I. chiriquensis* Standley
- 8b. Leaves chartaceous to coriaceous, (6–)8–40 cm long, elliptic, secondary venation distinct; staminate cymes branched.
- 10a. Leaves (6–)8–13 cm long, 4–7.5 cm wide with 6–8 secondary veins per side; fruit 0.3–0.6 cm long 9. *I. yurumanguinis* Cuatrecasas
- 10b. Leaves 15–40 cm long, 10–13 cm wide, with 10–15 secondary veins per side; fruit 0.8–1 cm long 10. *I. maxima* W. J. Hahn

1. *Ilex costaricensis* J. D. Smith, Bot. Gaz. (Crawfordsville) 57: 416. 1914. TYPE: Costa Rica. Puntarenas: Cuesta de la Cara, haud procul ab El Páramo, *Pittier 10183* (erroneously cited as *Pittier 10843* in original publication) (holotype, US 1380596).

Ilex valerii Standley, J. Wash. Acad. Sci. 16: 483. 1926. TYPE: Costa Rica. Heredia: Cerros de Zurquí, NE of San Isidro de Las Vueltas, *Standley & Valerio 50582* (holotype, US 1251513; isotype, K).

Ilex brenesii Standley, Field Mus. Nat. Hist., Bot. Ser. 18: 629. 1937. TYPE: Costa Rica. Entre La Palma y El Socorro de San Ramón, *Brenes 6226* (holotype, F).

Ilex ramonensis Standley, Field Mus. Nat. Hist., Bot. Ser. 18: 630. 1937. TYPE: Costa Rica. Entre Pata de Gallo y Santiago de San Ramón, *Brenes 6639* (holotype, F).

Ilex costaricensis is known throughout the Tala-

manchas of western Panama and eastern Costa Rica through the Cordillera Central of Costa Rica and on Volcán Mombacho in Nicaragua. In Panama, the species occurs at elevations of 1,200–1,700 m; flowering mostly in August.

Distinctive characters of *Ilex costaricensis* include epunctate leaves, attenuate leaf bases, leaf margins entire and strongly revolute at the base and along the petiole, the blade drying black or dark brown, lenticellate stems drying dark brown to black, inflorescences solitary and axillary, and capitate stigmas prominent in flower and fruit.

Edwin (1968) treated *Ilex valerii* from Costa Rica as a distinct species and included *I. ramonensis* Standley as a variety. *Ilex costaricensis* was apparently overlooked by Edwin, as he failed to mention the taxon in his treatment. The similarities between the types of these three taxa are numerous

and clearly support recognition of a single species. The type specimen of *Ilex brenesii* (Brenes 6266) is extreme in petiole, peduncle, and pedicel lengths, which are 3–10 times that found on other specimens of *Ilex costaricensis*. However, all other characteristics of the specimen agree with the type of *Ilex costaricensis* and fall within the range of variation accepted for that species. Smith (1914) placed *Ilex costaricensis* close to *I. mexicana* Hemsley based on apparent similarities in the inflorescences.

Collections from Cerro Colorado, Chiriquí, on the Continental Divide (Folsom *et al.* 4755, McPherson 8807, and Mori & Dressler 7895) have smaller, thinner, narrowly elliptic to lanceolate leaves with the margin revolute at the base and along the portion attenuate to the petioles. Occasionally a few spines are present on the leaves. These differences are consistent among all collections from Cerro Colorado and are perhaps related to local environmental conditions, such as the high copper concentrations of the substrate. The specimen from Cerro Hornito (Croat 67961) is similar to the type, however, and to most Costa Rican material.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Cerro Colorado, McPherson 8807 (MO, PMA). CHIRIQUI: Cerro Hornito, Croat 67961 (G, MO); Cerro Colorado, Folsom *et al.* 4755 (K, MO, PMA); Cerro Colorado, Mori & Dressler 7895 (F, MO, NY, PMA, US, NY).

2. *Ilex guianensis* (Aublet) Kuntze, Rev. Gen. Pl. 1: 113. 1891. *Macoucoua guianensis* Aublet, Hist. Pl. Gui. Fr. 88, t. 34. 1775. *Ilex acuminata* Willdenow, Sp. Pl. 1: 711. 1798. *Ilex macoucoua* Persoon, Syn. Pl. 1: 152. 1805. TYPE: French Guiana, Aublet *s.n.* (holotype, P in herb. Rousseau, vol. 3, folio 100). Figure 1.

Ilex panamensis Standley, Field Mus. Nat. Hist., Bot. Ser. 4: 221. 1952. TYPE: Panama. Bocas del Toro: Cooper 469 (holotype, F 579403; isotype, K).

Ilex gentlei Lundell, Field & Laboratory 13: 5. 1945. TYPE: Belize. Toledo, Punta Gorda–San Antonio Road, Gentle 4807 (holotype, SMU not seen; photo, MO; isotype, K).

Although somewhat variable, this species is characterized by its epunctate, coriaceous, spatulate to obovate leaves with entire, revolute margins and obscure secondary venation. While in flower, the cymes are borne on brachyblasts, which later expand as fruits mature resulting in clearly lateral or axillary cymes.

Of the species native to Panama, *Ilex guianensis* has the widest distribution, ranging from the Guianas through Venezuela and Colombia along the Carib-

bean coast of Central America to Tobasco, Mexico, and apparently throughout the Greater Antilles (Bornstein, 1989). It is also a major component of the vegetation of the Pearl Islands off the Pacific Coast of Panama (Johnston, 1949), illustrative of the numerous Caribbean species found on these islands (Bennet, 1968; D'Arcy, 1977). Flowering in Panama occurs during the major dry season of December to April, with scattered occurrence at other times of the year, particularly for upland populations.

Closely related congeners forming Loesener's section *Micranthae* subsect. *Epunctatae* are among the most variable and widespread within the genus (Bornstein, 1989). Previous studies of this group include a discussion of the relationships between *I. guianensis* and the widespread Caribbean taxon *Ilex sideroxyloides* (Swartz) Grisebach (Bornstein, 1989), and a limited study of the group as found in northern Central America (Hahn, 1988). Further study of the limits of variation in this group of species, particularly in the Greater Antilles and in northern South America, would help in establishing species delimitations and relationships. In the present work, the species is treated as known from Central America and the Guianas; synonymy is limited to Central America.

The presumably natural habitat for *I. guianensis* is sclerophyllous forest on seasonally dry, coastal or inland savannas typical of the type localities of Cayenne and Sinamarry, French Guiana, cited by Aublet. A similar sclerophyllous habitat with strong Caribbean affinities is also seen in the Pearl Islands, where most collections of the species in Panama have been made. The greatest degree of intraspecific variation, however, typically arises in recently disturbed areas at higher elevations. Such middle-elevation populations in Panama are known from Cerro Jefe, Cerro Campana, Cerro Azul, Boquete, and El Valle de Anton, all zones of deforestation within the last few hundred years (Bennet, 1968; D'Arcy, 1977).

A number of other species closely related to *Ilex guianensis* have been described from Colombia (e.g., *I. uniflora* Benthham and *I. danielis* Killip & Cuatrecasas), which may represent high-elevation morphs as found in Panama. *Ilex guianensis* is apparently replaced in the Amazon Basin by the related *I. inundata* Poeppig.

Reports of *Ilex occidentalis* Macfayden from Ancon Hill (Hemsley, 1880; see also Standley, 1929), based on Seemann 554, and *Ilex bumelioides* Kunth (Hemsley, 1880), based on Duchassaing *s.n.*, were founded on erroneous species concepts held by these authors (see Triana, 1872; Loesener, 1901), as

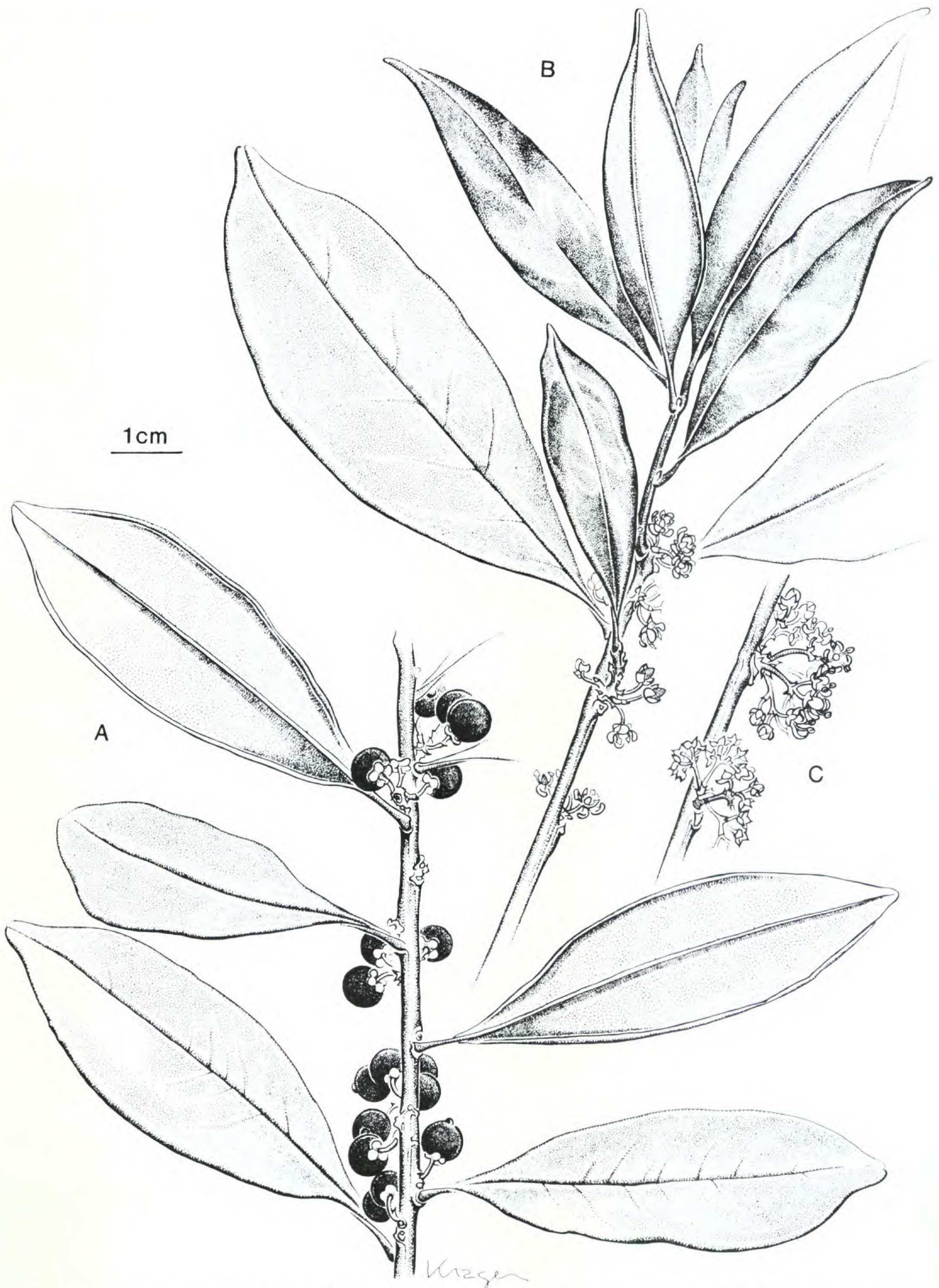


Figure 1. *Ilex guianensis* (Aublet) Kuntze. —A. Habit in fruit (Johnston 224). —B. Habit in pistillate flower (Gentle 1244). —C. Habit in staminate flower (Erlanson 411).

these collections clearly represent *Ilex guianensis*. The type of *Ilex bumelioides* Kunth is from Ecuador; the species is more closely related to *I. kunthiana*, while *Ilex occidentalis* Macfayden of Jamaica is probably synonymous with *I. guianensis*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante, Bocas Island, *Cooper 469* (F, G, K, NY); Chiriquí Lagoon, *von Wedel 1144* (GH, MO). CHIRIQUI: Llanos Francia, *Dwyer & Lallathin 8698* (MO, NY); El Boquete, Holcomb's Trail, *Killip 3562a* (US); Boquete, Llanos Francia, *Stern et al. 1197* (GH, MO). COCLE: El Valle, *Allen 752* (GH, MO); hills S of El Valle de Anton, *Allen 2505* (MO, NY, US), *Allen 3570* (F, G, GH, K, MO, NY, P, US); Penonome, *Dwyer 2017* (MO); between El Cope and sawmill on Continental Divide, *Hammel 2645* (MO, NY). COLON: along ocean trail between Río Indio and Miquel de la Borda, *Croat 36916* (MO), *Croat 36920* (MO); Salud, *Lao & Holdridge 229* (MO); trail above Río Indios, *Sullivan 113* (MO). HERERRA: 10 km W of Las Minas on road to El Toro, *D'Arcy & Sytsma 14319* (MO), *Sytsma & D'Arcy 3245* (MO); Las Minas, *Stern et al. 1807* (MO). LOS SANTOS: road to El Cortezo, *D'Arcy & Sytsma 14356* (MO, NY). PANAMA: Cerro Jefe, *Churchill 4284* (BM, G, MEXU, MO, PMA), *D'Arcy et al. 15500* (G, MEXU, MO, PMA) *D'Arcy et al. 15506* (G, MEXU, MO, PMA); ibique in monte Lancon iuxta urbem ipsem, *Duchassaing s.n.* (A); Cerro Campana, *Duke 10724(3)* (MO, OSU); Isla del Rey, *Duke 9519* (MO); Cerro Azul, *Dwyer 4087* (MO), *Dwyer 4700* (MO); San José Island, *Erlanson 77* (G, GH, NY, US), *Erlanson 260* (G, P, US), *Erlanson 348* (G, GH, NY, US), *Erlanson 411* (GH, US), *Erlanson 513* (GH, US); Cerro Jefe, *Folsom et al. 2516* (MO, PMA); Cerro Azul, *Gentry & Dwyer 3408* (DUKE, F, NY); San José Island, *Harlow 95* (GH, US), *Johnston 224* (DUKE, GH, US), *Johnston 338* (GH), *Johnston 341* (BM, GH, MO, US), *Johnston 426* (GH, MO, US), *Johnston 428* (DUKE, GH); Cerro Jefe, *Mori 6529* (MO), *Mori 6531* (MO, NY), *Pipoly 7018* (MO); without locality (cited in Hemsley (1879) as Mount Lancon (Ancon Hill), near the city of Panamá) *Seemann 554* (K); Cerro Campana, *van der Werff & Herrera 6153* (DUKE, G, K, MEXU, MO, NY, PMA), *van der Werff & van Harvelde 6916* (MEXU, MO, PMA); Playa Corona, *Vargas, Jr. 15* (MO). VERAGUAS: Escuela Agrícola Alto de Piedra, *Croat & Folsom 33978* (MO).

3. *Ilex fortunensis* W. J. Hahn, sp. nov. TYPE: Panama. Chiriquí: La Fortuna hydroelectric project, in cloud forest, along trail uphill behind camp, 1,200–1,400 m, *Hammel 2164* (holotype, MO 3488625; isotypes, PMA, US).

Frutex; caules lenticellis praediti; folia integra, tenuicoriacea, glabra, valde bicoloria, epunctata; inflorescentiae pistillatae ramosae 2 ordine dispositae; stigma quadrilobatum; fructus globosi, 9–10 mm × 7–10 mm.

Shrub, 4 m tall, moderately branched. Stems terete, somewhat ridged when young, covered with fine white pubescence, young stems drying dark brown or black; lenticels small and sparse or absent; bark dark gray-brown, smooth to somewhat rough with numerous round or oval lenticels, 1–2 mm diam.; stipules broad-triangular, 0.4–0.8 mm long,

0.8–1.4 mm wide, deciduous. Leaves thin coriaceous, glabrous, drying dark olive green adaxially, pale yellowish tan abaxially, epunctate, elliptic to obovate-elliptic, (5–)7–9(–11) cm long, 3.5–5 cm wide, apex caudate to acute, base shortly attenuate, margins entire, sometimes very slightly revolute; venation brochidromous, somewhat eucamptodromous at the base, the secondary veins 5–7 per side, the tertiary veins reticulate, apparent; petioles 0.5–1 cm long, 0.8–1.2 mm diam., round in cross section, caniculate adaxially, drying black. Staminate inflorescences not known. Pistillate inflorescences not known in flower, only in fruit where they are axillary or lateral simple cymes on new wood, branched to 2 orders with 3 fruits per inflorescence; bracts ovate-triangular, ca. 2 mm long, thick coriaceous; peduncles 0.5–1 cm long, 1–1.5 mm wide, flat in cross section, tapering toward the apex; peduncular bracts triangular, 0.5–0.8 mm long, 0.8–1 mm wide, paired laterally at the first furcation; pedicels 2–5 mm long, square or angled in cross section; bracteole absent. Fruit globose, 9–11 mm long, 7–10 mm diam.; sepals 4–5, oblong or rounded; pericarp coriaceous, 0.3–0.5 mm thick, deep red to purple drying black-purple, the stigma four-lobed, 3.5–4.5 mm diam., spreading, not prominent in profile; mesocarp copious; immature pyrenes 4, trigonal.

Ilex fortunensis is known only from the type collection from the La Fortuna hydroelectric site in Chiriquí at an elevation of 1,200–1,400 m. This collection bears immature fruits collected in March.

The species is distinguished by the inflorescence type and the distinctly discolored, thin coriaceous leaves with entire margins. The infructescences are borne on relatively young stems, suggesting that the inflorescences were clustered on an abbreviated stem while flowering.

4. *Ilex pallida* Standley, J. Wash. Acad. Sci. 16(18): 482. 1926. TYPE: Costa Rica. Heredia: Cerros de Zurquí, NE of San Isidro, 2,300 m, *Standley & Valerio 50608* (holotype, US 1251651; isotype, F). Figure 2.

Ilex pallida is found throughout the Talamanca of Panama and Costa Rica and on nearby mountains at 2,000–3,000 m, and on Volcán Mombacho in Nicaragua above 1,100 m. The species flowers late in the Panamanian dry season, February to April, and again during the brief intermittent dry spell of June to August. Fruits are borne in March and September in Panama and Costa Rica, more sporadically in Nicaragua.

The species is characterized by the epunctate leaves, consistently spinose margins with small but

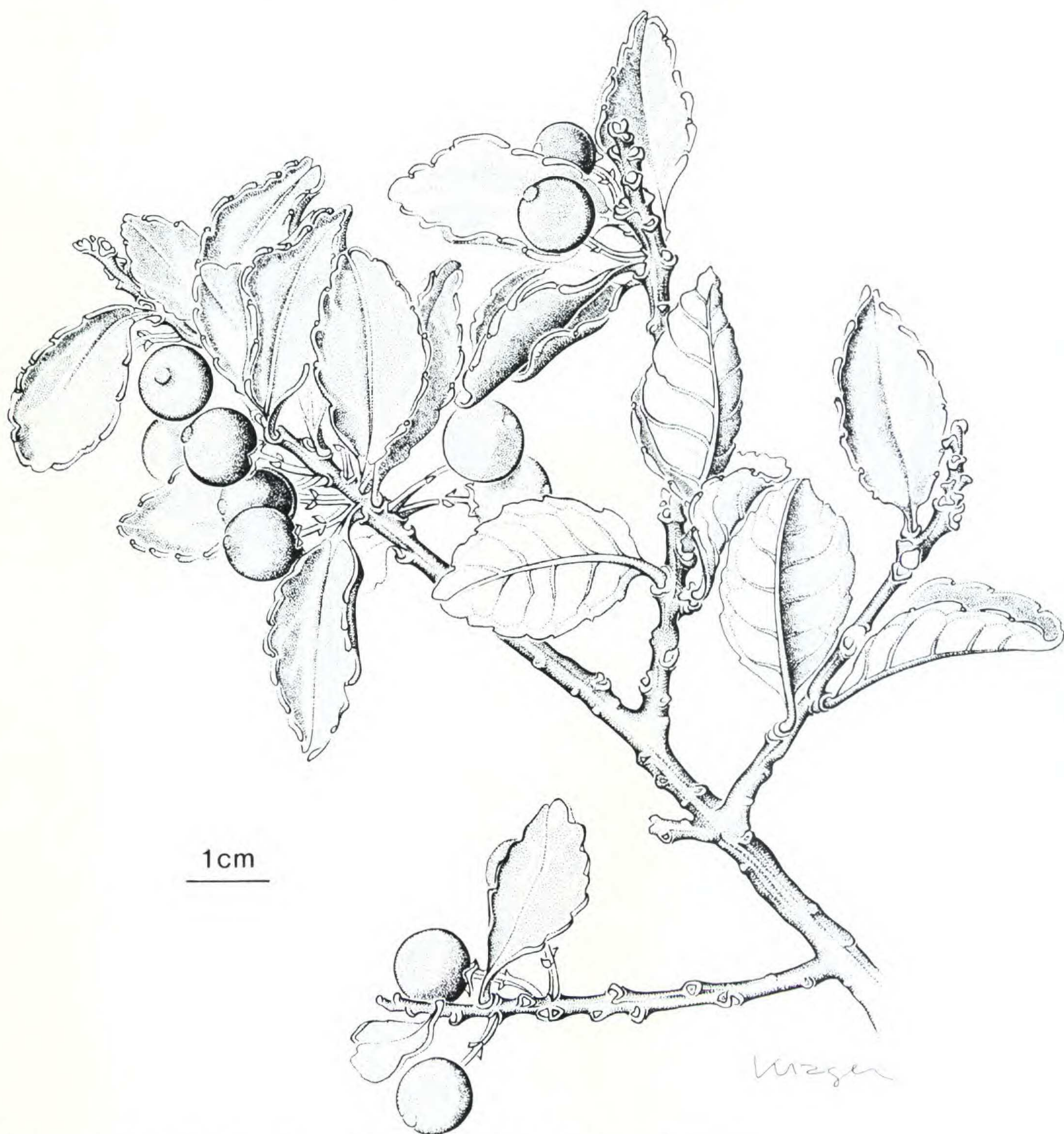


Figure 2. *Ilex pallida* Standley. —Habit in fruit (D'Arcy & Hammel 12496).

evident serrations or crenulations, the blade drying green or olive, pistillate inflorescences with solitary flowers and fruits, and the fruits to 1 cm long and 0.8 cm in diameter. Most collections from the Talamanca have relatively thin leaves.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Valle de Silencio, *Antonio 1599* (G, K, MO, PMA); 6 km NW of Cerro Enchandi, *Davidse et al. 25237* (CR, G, MO). CHIRIQUI: El Volcán, *D'Arcy & Hammel 12496* (MO, PMA, US); Bajo Chorro, *Davidson 254* (F, MO); Volcán Baru, *Hammel et al. 6446* (PMA); Aguacata, *Hammel et al. 7019* (A, F, MO, NY, PMA); Bajo Chorro, *Wilbur et al. 17276* (DUKE).

5. *Ilex lamprophylla* Standley, J. Wash. Acad. Sci. 15(21): 476. 1925. *Ilex discolor* Hemsley

var. *lamprophylla* (Standley) Edwin, Ann. Missouri Bot. Gard. 53: 376. 1966. TYPE: Costa Rica. Cartago: La Estrella, *Standley 39410* (holotype, US 1228657; isotypes, A, K). Figure 3.

Ilex carpintera Standley, J. Wash. Acad. Sci. 15(21): 477. 1925. TYPE: Costa Rica. Cartago: Cerro de La Carpintera, *Standley 34491* (holotype, US 1226682).

Ilex tristis Standley, J. Wash. Acad. Sci. 16(18): 482. 1926. TYPE: Costa Rica. San José: Cerro de las Vueltas, *Standley & Valerio 43670* (holotype, US 1251406).

Ilex davidsoniae Standley, Field Mus. Nat. Hist., Bot. Ser. 22: 88. 1940. TYPE: Panama. Chiriquí: Bajo Chorro, Boquete District, *Davidson 166* (holotype, F 915592; isotypes, A, MO, US).



Figure 3. *Ilex lamprophylla* Standley. —A. Habit in fruit (Standley 39440). —B. Fruits (Standley 39440).

Usually found above 1,500 m elevation, this species is particularly abundant in the Cordillera Central of Costa Rica, with extensions into the Talamancas of Costa Rica and Panama and on scattered peaks

in Nicaragua and El Salvador. Flowering in Panama occurs at the end of the wet season through the dry season, September to March.

Ilex lamprophylla is readily recognized by its

normally rounded leaf crenulations, epunctate leaves, which frequently dry a dark brown color, lighter brown abaxially, cymes on a reduced stem, which later expands in fruit, and the deeply grooved pyrenes, which give a ribbed appearance to the mature fruits.

Ilex davidsoniae and *Ilex carpintera* were considered by Standley to be possibly synonymous with *I. lamprophylla*. Study of a large array of specimens supports this view. Standley (1926, 1937) also expressed doubts about the validity of his *Ilex tristis*, which he cited as known only from the type locality of Cerro de las Vueltas, San José Province, Costa Rica. A search for this taxon in the region proved fruitless, and I consider it to be merely an immature specimen of *I. lamprophylla*.

Edwin (1968) recognized *I. lamprophylla* as a variety of the Mexican *I. discolor*, citing *I. carpintera* and *I. davidsoniae* as synonyms. In addition, a number of herbarium specimens from Central America have been annotated by Edwin with *I. discolor* Hemsley var. *tristis* (Standley) Edwin, and *I. discolor* Hemsley var. *hondurensis* (Standley) Edwin. No reasons were given for this transfer, although there is some gross similarity in leaf shape and inflorescence arrangement. *Ilex lamprophylla* differs from *I. discolor* in its thinner, broader, epunctate leaves that dry a dark brown or black, the nature of the brachyblast, the branching and size dimensions of the inflorescence, and in the texture of the fruits and pyrenes.

Two collections from Chiriquí, *McPherson 8946* and *Mori & Kallunki 6000*, are unusual in that the leaves, apparently immature, are relatively thin with much reduced crenulations and a few small marginal spines.

Additional specimens examined. PANAMA. CHIRIQUI: Cerro Punta, *Lao 332* (MO), *Luteyn 3085* (DUKE); Bajo Chorro, *Davidson 166* (A, F, MO, US); N of San Felix, *Mori & Kallunki 6000* (MEXU, MO, PMA); Fortuna Dam, *McPherson 9095* (MEXU, MO, PMA); Cerro Colorado, *McPherson 8946* (MEXU, MO, PMA). COCLE: El Valle, *Sytsma 3824* (MO, PMA).

6. *Ilex stellata* W. J. Hahn, sp. nov. TYPE: Panama. Veraguas: vicinity of Cerro Arizona–Tute, above Sante Fé and Altos de Piedra, *McPherson 12806* (holotype, MO 3821597; isotypes: G, K, PMA, WIS).

Arbor; folia bullata tomentosa pilis tomentosis, epunctatis, 5–9 cm longa, 3–5 cm lata; petioli 1–2 cm longi; inflorescentiae pistillatae ramosae; stigma manifeste elevato-capitatum.

Tree to 8 m tall; moderately ramified. Stems slightly ridged on new growth, equally so on older

growth, lightly beset with fine tan or white stellate and simple hairs, drying yellowish tan or greenish brown; lenticels scattered, raised, oval, ca. 1 mm long; bark dark grayish to grayish brown, moderate, ridged, densely covered with raised oval lenticels to 1 mm long; stipules triangular, ca. 1 mm long, extensions of the bark. Leaves coriaceous, strongly and deeply bullate, densely pubescent with short, white, stellate hairs, becoming glabrous with age except along the veins abaxially and on the petiole, drying brown to dark brown, epunctate, ovate to obovate, 5–9 cm long, 3–5 cm wide, apex rounded to obtuse, slightly acuminate, base obtuse, short attenuate, margin strongly revolute, essentially entire but with numerous minute teeth along the margin, scarcely visible; venation brochidodromous, the secondary veins 5–7 per side, deeply sunken adaxially, prominent and raised abaxially, the tertiary veins reticulate and distinct; petioles 1–2 cm long, 1–2 mm wide, densely covered with short, white, stellate hairs. Staminate inflorescence not seen. Pistillate inflorescence not seen in flower, in fruit of solitary axillary cymes borne on new wood, branched to 2 or 3 orders with 3–7 flowers per dichasium; bracts ca. 1 mm long, triangular, deciduous; peduncle 5–10 mm long, 1–2 mm wide, flat in cross section; peduncular bract triangular, awl-shaped, ca. 1 mm wide and long, laterally paired or slightly offset at the first furcation; rachis 0.2–1 cm long, 1–1.5 mm wide, flattened or angular; bracteoles 0.5 mm long; pedicels 2–8 mm long, ca. 1 mm wide, angular, tapering toward the base; floral bracteoles apparently absent. Immature fruits depressed globular; sepals 5, explanate in fruit, rounded to ovate, 1–1.5 mm long; pericarp leathery, green, the stigma prominent, raised; mature pyrenes unknown.

The species is endemic to Panama and known only from elfin or summit forest at 1,000–1,200 m elevation on Cerros Caracoral and Gaital in Coclé and Cerros Arizona and Tute in Veraguas Province.

Ilex stellata is readily recognized by the deeply bullate leaves, which bear a moderately thick covering of stellate hairs. *Ilex bullata* Cuatrecasas, described from Valle, Colombia, resembles *I. stellata* with its deeply bullate leaves, but differs in possessing simple hairs, smaller leaves (3–6 cm long, 1.5–3 cm wide) with abaxial punctations, shorter petioles (3–5 mm long), unbranched pistillate inflorescences, and an adpressed capitate stigma. The infructescences are borne solitary and axillary on young stems, suggesting that the cymes are clustered in flower as with *I. lamprophylla*.

Paratypes. PANAMA. COCLE: Cerro Caracoral, *Kirk-*

bride, Jr. 1110 (MO); above El Valle, on trail to top of Cerro Gaital, *McPherson 11958* (F, K, MO, PMA, US).

- 7. *Ilex vulcanicola*** Standley, J. Wash. Acad. Sci. 15(21): 477. 1925. TYPE: Costa Rica. San José: Las Nubes, *Standley 38729* (holotype, US 1228373).

Ilex vulcanicola is restricted to the highlands of western Panama and Costa Rica at elevations above 1,800 m. This species is related to the widespread, polymorphic *Ilex kunthiana* Triana of Colombia, which differs in having solitary cymes as opposed to the consistently clustered cymes found in *I. vulcanicola*. Other species described from northern South America, such as *I. farrolensis* Cuatrecasas and *I. caniensis* MacBride, are also closely related and together would probably be referable to series *Paltoria* sensu Loesener (1901, 1908). Individuals with extremely large leaves might be confused with *I. chiriquensis*, which differs in its generally larger leaves and fruits and in having more cymes per fascicle. In Panama, flowering of *I. vulcanicola* is sporadic from February to August.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Fortuna Dam, *McPherson 11079* (MO, PMA, US). CHIRIQUI: between Gualaca and Fortuna Dam, *Croat 49956* (MO, NY, PMA, US); La Fortuna, *Hammel 6243* (F, MO, NY, US); between Los Planos de Hornito and Fortuna Dam, *Hampshire & Whitefoord 251* (BM), *Hampshire & Whitefoord 258* (BM). COCLE: Cerro Pilon, *Dwyer & Lallithin 8646* (F, MO, NY); Cerro Gaital, *Knapp et al. 5990* (G, MO, PMA, MEXU); La Mesa, *McPherson 11253* (MO, PMA, US); Cerro Caracoral, *Sytsma 4049* (A, MO, NY, PMA, US). PANAMA: Cerro Campana, *Croat 35973* (F, MO); Cerro Jefe, *Mori & Kallunki 6088* (MO); Cerro Campana, *Mori & Bolten 7694* (F, MO, NY, OSU, US); Cerro Jefe, *Tyson et al. 4362* (F, MO). VERAGUAS: Cerro Tute, *Mori et al. 7594* (A, F, MO, NY, PMA), *Sytsma & Andersson 4691* (A, F, MO, US).

- 8. *Ilex chiriquensis*** Standley, Pub. Field Mus. Nat. His., Bot. Ser. 22: 88. 1940. TYPE: Panama. Chiriquí: Bajo Chorro, Boquete District, 1,800 m, *Davidson 243* (holotype, F 915550; isotypes, MO, US).

Ilex chiriquensis is largely confined to western Panama and Costa Rica, with outlying populations known at the Monteverde area of western Costa Rica. Populations in Panama are typically found at elevations of 1,500–2,000 m. Collections from the Fortuna Dam area are known from ca. 1,100 m and from Monteverde, Costa Rica, from 2,000 to 2,500 m. The flowering period of *I. chiriquensis* is in March and April, with fruiting from May to August.

This species is distinguished by its medium-sized,

thickly coriaceous, orbicular to elliptic leaves, unbranched staminate inflorescences, and depressed capitate fruit. It is sometimes difficult to separate from *Ilex yurumanguinis* but that species typically occurs at lower elevations and has thinner, larger, elliptic leaves with distinct secondary venation, branched staminate inflorescences, and ovoid-capitate fruits. Populations of *I. chiriquensis* from Monteverde, Costa Rica, have relatively distinct secondary venation and more pronounced marginal teeth. An undescribed epiphytic taxon from Costa Rica appears to be closely related to *I. chiriquensis*, but differs in its consistently narrower, obovate leaves.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río Culebre, *Gomez et al. 22387* (CR, G, MO); Chiriquicito–Calderas Trail, *Kirkbride & Duke 993* (MO). CHIRIQUI: between Fortuna Lake and Chiriquí Grande, *Croat & Grayum 59994* (MO, PMA); Bajo Chorro, Boquete, *Davidson 243* (F, MO, US); Palo Alto NE of Boquete, *Hammel 6066* (MO); Cerro Hornito, *Hammel 6219* (MO, NY, PMA); Cerro Punta, *Hammel et al. 6532* (MO); Palo Alto, *Hammel 7449* (MO); Cerro Horqueta, *Luteyn & Wilbur 4609* (DUKE); Cerro Pate Macho, *McPherson 8058* (MEXU, MO, PMA); Cerro Hornito, *Mori 7504* (BM, MEXU, MO, PMA); Cerro Punta, *van der Werff & Herrera 6311* (G, MO); Cerro Horqueta, *Wilbur & Luteyn 19332* (DUKE). VERAGUAS: Cerro Tute, *Mori et al. 7599* (BM, MO).

- 9. *Ilex yurumanguinis*** Cuatrecasas, Lloydia 11(3): 210. 1948. TYPE: Colombia. Valle: Río Yurumanguí, Veneral, bosques en la Quebrada del Zancudo, 10–50 m, 10 Feb. 1944, *Cuatrecasas 16156* (holotype, US 1951538; isotype, F).

This species occurs in wet forests from sea level to 1,500 m in Panama through northwest Colombia into Ecuador, with an outlying population on the Cocos Islands. In western Panama, the species flowers at the end of the dry season from (December) February to April and fruits in July and August. Populations in central and eastern Panama flower slightly earlier (November to February).

Collections from eastern Panama (Colón, Darién, Panamá, and San Blas) from below 500 m elevation are virtually identical to material from the type locality of the Río Yurumanguí in Valle, Colombia, with thick leaves, distinct rounded crenulations, a rounded, obtuse apex, and revolute margins.

Populations from elevations of 700–1,000 m in Coclé and 1,000–1,500 m in Chiriquí and Bocas del Toro are characterized by thinner leaves that dry strongly bicolored, the leaf apex long acuminate, the marginal crenulations less rounded or laterally flattened and almost entire with only a few scattered spines, thinner pedicels and peduncles, and more

delicate cymes. These specimens approach *I. maxima* in leaf shape but have much smaller leaves with fewer secondary veins, smaller fruits, and different flowering and fruiting times. These populations perhaps deserve specific status, but further study of the Colombian taxa is still needed.

One unusual collection from the ridge of Cerro Caracoral (*Sytsma 3824*) shows strongly reduced, spatulate leaves and denser ramification, possibly due to the windswept habitat.

Two collections from Bocas del Toro near the Fortuna Dam site (*McPherson 9050B* and *Croat 59994*) show such features as broader and thicker leaves and more grayish bark, which approach *I. chiriquensis*. These two gatherings were made in the vicinity of *McPherson 9050A* and *Croat 59995*, which fall well within the morphological range of the upland *I. yurumanguinis* form. These may be hybrids, as both species are found in the area.

Cuatrecasas placed *I. yurumanguinis* near *I. laureola* Triana and *I. affinis* Gardner, two species relegated by Loesener (1901, 1908) to series *Thyr-siprinus* sect. *Thyr-siflorae*.

Additional specimens examined. PANAMA. CHIRIQUE: road from Fortuna Lake to Chiriquí Grande, *Hampshire & Whitefoord 425* (BM); 1 km N of Fortuna Lake, *Hampshire & Whitefoord 940* (BM); Fortuna Dam, *McPherson 8731* (MEXU, MO, PMA), *McPherson 9125* (MEXU, MO, PMA); Boquete, Fortuna Dam site, *van der Werff & van Harvelde 6815* (G, MO, PMA). COCLE: Cerro Caracoral, *Duke & Dwyer 15078* (MO, NY); above El Valle, *McPherson 12151* (BM); La Mesa, *Nee & Dwyer 9157* (DUKE, F, MO, OSU, PMA, US); Cerro Caracoral, *Sytsma 3824* (MO). COLON: East Ridge, *Duke 15270* (MO). BOCAS DEL TORO: Finca Serrano, NE of Boquete, *Hammel 6168* (DUKE, MO, NY, PMA, US); Fortuna Dam Forest, *McPherson 9050* (MEXU, MO, PMA). DARIEN: S of Garachineon W slope of Serrania Sapo, *McPherson et al. 15379* (MO). PANAMA: Rancho Chorro, Torti Arriba, *Folsom et al. 6712* (MO, NY); El Llano-Carti Road, km 16-18.5, *Nee & Tyson 10957* (MO). SAN BLAS: trail along Continental Divide, *McDonagh et al. 302* (BM, MO).

10. *Ilex maxima* W. J. Hahn, sp. nov. TYPE: Panama. Coclé: La Mesa, 4 km N of El Valle, 875 m, *Nee & Hale 9626* (holotype, MO 38211595; isotypes, BM, F, G, MEXU, PMA, US). Figure 4.

Arbor; caules arcuati; folia tenui-coriacea, punctata, 15-40 cm longa, 10-15 cm lata; inflorescentiae dichasiis fasciculatis; inflorescentia staminata ramosa; inflorescentia pistillata non ramosa.

Tree to 10 m tall, laxly ramified, the branches often arching. Stems slightly angular-ridged when dry, glabrous; lenticels scattered on young stems, abundant on older stems, oval, split, 0.6-1.3 mm

long, 0.3-0.7 mm wide; bark thin, tannish gray; stipules to 2 mm long, appearing as extensions of bark. Leaves thick chartaceous to coriaceous, drying dark brown-green adaxially, pale tan abaxially, mostly glabrous, punctate abaxially, elliptic, 15-40 cm long, 10-15 cm wide, the apex acute, the base attenuate, the margin laterally flat, subentire with occasional spines, very slightly crenulate toward the apex; venation strongly brochidodromous, the secondary veins 10-20 per side, the tertiary veins reticulate, distinct; petioles thickened, 1.5-2 cm long, drying black or dark brown. Staminate inflorescence of compound cymes borne on a much reduced stem resembling an axillary panicle; cymes branched to 2 orders, 1-3 flowers per inflorescence, bracts coriaceous, scale-like, ovate-rounded, 1-2 mm long, 1-1.5 mm wide; peduncle 0.5-1 cm long, 0.4-0.6 mm wide, laterally flattened; peduncular bracts triangular, ca. 1 mm long, 0.5 mm wide, induplicate folded, oppositely paired or distinctly offset; pedicels 0.3-1 cm long, 0.3-0.4 mm wide, laterally flattened; floral bracteoles paired at the base of the pedicels, small. Pistillate inflorescences of unbranched cymes clustered on a much reduced stem with the complete ensemble resembling a cyme, the stem not expanding in fruit; 1 flower per dichasium; bracts coriaceous, deltoid, 1-2 mm long, 1.5-2.5 mm wide; peduncle 0.8-1 cm long, 0.3-0.6 mm wide, flattened in cross section, tapering; peduncular bracts, paired or essentially so, membranaceous, deltoid, 0.8-1.2 mm long, 0.3-0.7 mm wide; pedicels 1-2 mm long, 0.1-0.2 mm wide, round in cross section; floral bracteoles minute. Staminate flowers 4-merous; calyx broad cupuliform, sometimes urceolate, the sepals glabrous, ovate-deltoid, 1.2-1.5 mm long, 1.2-1.5 mm wide, the margin mostly regular, induplicate folded; corolla rotate, the petals white, glabrous, 2-2.5 mm long, 1.5-2 mm wide, the margin entire; filaments 2-2.5 mm long, flattened, tapering, the anthers yellow, ovoid, tapering, 1-1.5 mm long, 0.3-0.6 mm wide; pistillodia spherical-conical, 0.4-0.6 mm tall, 0.8-1.2 mm diam., the stigma cylindrical, 0.1-0.3 mm tall. Pistillate flowers unknown. Fruit spherical to ellipsoid, 0.8-1 cm long, 0.5-0.7 mm diam.; pericarp leathery, moderately thick, dark purple at maturity, stigma persistent, spreading to slightly flattened capitate, 2-2.5 mm diam., 1 mm high, 4-lobed; mesocarp moderately thick, fleshy; pyrenes 4, trigonal 4 mm long, 1-1.5 mm wide, shallowly channeled, endocarp bony.

Ilex maxima occurs in wet forest in the Cordillera Central of Costa Rica, the Talamancas of Costa Rica and Panama through central Panama to the western slopes of the Andes in Colombia. It generally occurs



Figure 4. *Ilex maxima* W. J. Hahn. —A. Habit (Nee & Hale 9626). —B. Fruits (Stevens 18321).

at elevations of 700–1,000 m, except to 1,500 m in the Talamanca and lower elevations in Colombia. Flowering is at the end of the wet season into the onset of the dry season, from September to November, and fruiting is from January to April.

Ilex maxima is characterized by its lax habit, cymes borne clustered on reduced stems in flower and fruit often appearing cauliferous, the large spherical fruits, and the very large, elliptic leaves. It is closely related to *I. tatei* of the Guayana Highland region of Venezuela and *I. yurumanguinis* Cuatrecasas of northwestern Colombia and Panama, but differs in its larger and relatively thicker leaves with more secondary veins, the larger, more robust staminate inflorescences, and the larger fruits. Other apparently related taxa include a number of Colombian species such as *I. caliana* Cuatrecasas and *I. laurina* Kunth, which have been referred to section *Daphnophyllae* (Loesener, 1901, 1908).

Paratype. PANAMA. CHIRIQUI: confluence of the Río Hornito and Río Chiriquí, *Stevens 18321* (MO, UTD).

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